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Bulletin

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The development of the embryo of Kochia scoparia

MARION E. WILLIAMS

(WITH PLATES 25 AND 26)

INTRODUCTION

The study of the development of the embryo of *Kochia scoparia* (L.) Roth was suggested because of the transparent seed coats in this species. The embryo, lying in a watery embryo-sac, may be distinctly seen in a seed which is under the dissecting microscope. For this reason, selection of embryos in successive stages of development is easily made; moreover, since the flowers appear as the stem elongates, mature seeds may be found on the same branch that bears unfertilized ovules.

Few of the Chenopodiaceae have been studied from the point of view of the development of the embryo. Comprehensive works on the embryo-sac by Dahlgren (1916) and Fischer (1880), on endosperm by Hegelmaier (1885), and on seed coats by Netolitzky (1926) include investigations on members of this family. Other studies dealing specifically with the Chenopodiaceae also emphasize these phases of seed study, only briefly describing the embryo. Extensive work has been done, however, by Souèges (1920) on the embryo of *Chenopodium bonus-henricus*. It is with this species, therefore, that *Kochia scoparia* is compared in this paper, with occasional reference to descriptions reported for other related genera and families.

MATERIALS AND METHOD

Material was collected throughout the summer and fall from both the cultivated plants and escapes. Ovules were removed under a binocular dissecting microscope and placed immediately into formalin acetic-alcohol.[1] Best results in fixation were obtained when the cells were completely water-filled. When collections were made in the afternoon, the flower-bearing branches were submerged in water for ten minutes and then placed in a moist chamber until the leaves were markedly turgid. After this treatment the embryo-sacs were less plasmolyzed and were more suitable for fixation. Some of the larger embryos were removed from the ovules before immersion in the fixing solution. Entire flowers and fruits were also preserved, although penetration through the many layers was too slow to give good results in fixation.

[1] Formula: 100 cc 50% alcohol
10 cc neutral formalin
7 cc glacial acetic acid

[THE BULLETIN FOR JUNE (59: 313–390) WAS ISSUED 15 JUNE, 1932.]

In preparation for imbedding in paraffin, the smaller ovules were lightly stained so that their position in the paraffin block might be more easily determined.

Old ovules and embryos were cut 5–8μ thick; young ovules and flowers, 8–12μ. Sectioning at any stage was extremely difficult. Young ovules tend to be spherical so that sections, intended as longitudinal cuts of the embryo sac, often proved to be transverse or oblique. Orientation of the older flattened ovules was less difficult, but due to the starch which filled the cells of the perisperm they did not section readily. This was remedied by trimming the paraffin block closely and placing it in water for a time, varying from one to three weeks.

THE OVULE

The ovule is that typical of the Chenopodiaceae and all other families of Engler's order Centrospermae. It is campylotropous, arising at the base of the ovary on a short funiculus that becomes longer and more slender as the ovule bends over it. Both the micropylar and chalazal ends of the ovule bend down toward the base of the funiculus which at the same time is pushing upward into the concavity. Finally the ends of the ovule come close together, often slightly overlapping, and within, the perfectly horseshoe-shaped embryo-sac encircles a region of perisperm.

In the young ovule (fig. 19), the two integuments are each composed of two layers, each layer one-cell thick. At the micropyle, the cells of the inner integument are much enlarged and extend beyond the margins of the outer integument. As the ovule develops, the integuments are stretched and digested until the identity of the cells may be entirely lost. A homogenous layer (fig. 20, d) is laid down between the nucellus and the inner integument, appearing before the formation of the embryo and becoming more pronounced as the ovule matures. By the Sudan III test, the presence of suberin in this layer was indicated. In sections, this layer was deeply stained by gentian-violet. The perianth parts, with the ovary wall, are retained about the seed at maturity.

THE EMBRYO-SAC

The embryo-sac is early buried deep in the nucellus, situated, as Hegelmaier (1885) describes, closer to the chalazal end of the ovule than to the micropylar end (fig. 19). A similar condition in *Chenopodium foetidum* is explained by Fischer (1880) as being due to the rapid division of a line of cells formed from the original tapetal cell. The arrangement of the cells in parallel rows in the micropylar region of the nucellus indicates that this same progression of cells may take place in *Kochia scoparia*.

The embryo-sac is of the normal eight-nucleate type as has been reported in *Chenopodium foetidum* by Fischer (1880), in *Atriplex hortensis* by Cohn (1914), in *Hablitzia tamnoides* by Dahlgren (1916), in *Salsola Kali* by Romell (1919), and in *Beta vulgaris* by Artschwager (1927). The antipodals disappear quickly and were observed in *Kochia scoparia* only in a disintegrated form. In this condition they were not easily distinguished from the adjacent cells of the nucellus which were being absorbed by the enlarging embryo-sac. The synergids, too, are short lived. They were however, identified in many sections, being long and narrow in outline and lying close to the egg. The polar nuclei fuse before fertilization. The nucleus thus formed is large with a brightly staining nucleolus and lies near, or in contact with, the egg nucleus. Apparently the embryo-sac remains in this stage for a long period, since most of the sections showed this two-nucleate condition. An identical embryo-sac is described by Gibbs (1907) for *Stellaria media* of the Caryophyllaceae. Early fusion of the polar nuclei is also described in *Chenopodium foetidum* by Fischer (1880).

The embryo-sac enlarges by digestion of the surrounding nucellar tissue even before the complete eight-nucleate condition is attained. After the formation of the endosperm nuclei the sac rapidly elongates, keeping far in advance of the embryo. The nucellus is finally absorbed almost to the chalazal end of the ovule, with but one or two nucellar layers remaining between the sac and the integuments.

THE ENDOSPERM

Division of the endosperm nucleus takes place before that of the fertilized egg. The resulting endosperm is free-nuclear as is reported by Hegelmaier (1885), forming a deeply staining cap over the suspensor (fig. 20), and later, the lower half of the embryo. By the time the cotyledons appear, wall formation has taken place in this micropylar region, the endosperm cells becoming conspicuously vacuolated. Sections did not verify Hegelmaier's statement that the endosperm reaches only two-thirds of the distance to the chalazal end of the sac. On the contrary, a second endosperm cap is formed at the chalazal end, remaining free-nuclear and digesting the tissue ahead of it (fig. 20). The elongation of the embryo-sac is brought about by the action of this portion of the endosperm.

Between the two caps the endosperm is at first but a peripheral layer of cytoplasm with a few scattered nuclei. As the embryo elongates, the cellular micropylar cap advances into this mid-region and slightly fills in the space between the cotyledons when the embryo is at the stage illustrated in figure 32. A peripheral layer of endosperm, one-cell thick, lines the remainder of the embryo-sac until it merges into the free-nuclear en-

dosperm which occupies the chalazal end. Thus the embryo is completely enclosed in a loose sac of endosperm which often remains about it when the embryo is lifted out from the ovule.

THE PROEMBRYO

The proembryo like that of *Chenopodium bonus-henricus* is markedly filamentous (figs. 1–10), a characteristic due to the number of transverse divisions that take place before the first vertical wall appears. The stage at which this vertical division is made varies but it usually occurs at or soon after the six-celled stage. Even then, contrasting with *Capsella* whose embryo was for a long time considered typical of dicotyledons, the vertical division of the apical cell is delayed until after such divisions have occurred in the cells in the several tiers below. Figure 8 shows an embryo in which longitudinal division has taken place in the fifth and seventh tiers but not in the upper four.

Figure 7 shows one in which the cells of the first and second tiers have divided vertically; in that shown in figure 9, a vertical wall occurs in the third tier also. The comparative development of the cells indicates that the apical cells have divided recently. In no case was a vertical wall seen in an apical cell only. In the embryo illustrated in figure 10, the upper three tiers have reached the same stage of development, having divided once in the plane parallel to the page and one of each pair of daughter cells having redivided in a plane at right angles to that of the previous division.

As in *Chenopodium bonus-henricus*, when the embryo proper becomes differentiated, the suspensor is seen to develop from two tiers which, in dividing, become four, the uppermost being the hypophysis (figs. 9, 10). The embryo proper develops from four tiers which are easily distinguished as the change from the linear to the spherical form takes place (figs. 9–12; 14–18). Souèges, however, describes the embryo of *Chenopodium bonus-henricus* as including but three tiers. This situation occurs as an occasional exception in *Kochia scoparia* as is shown in figure 13.

THE SUSPENSOR

The suspensor remains characteristically linear. The identity of the three cells below the hypophysis is soon lost by their multiplication into a long row of cells which vary in size and in number (figs. 11–17). Only rarely were the suspensor cells seen to have divided vertically. Two such exceptions are shown in figures 8 and 13. Maturing embryos, removed from the ovules, still retained a portion of the filamentous suspensor (figs. 29–34). In sections of the ovule, even in advanced stages, the row of cells was seen buried in the endosperm cap at the micropylar end. Only in the

mature seed when the endosperm had been obliterated was the suspensor lacking (fig. 35).

The basal cell of the suspensor is greatly enlarged and vacuolated in the early stages. It is buried in the nucellar tissue, as shown in figure 20, behind the endosperm cap which surrounds the rest of the suspensor. In later stages (figs. 11–17), it becomes irregular in shape and size as the nucellar tissue about it is digested by the endosperm. At the same time, adjacent cells of the suspensor may also become distorted.

It is in the structure of the suspensor that the only striking difference appears in the embryos of *Kochia scoparia* and *Chenopodium bonus-henricus*. Souèges' illustrations show the filamentous suspensor only up to the time the embryo is about four cells in diameter. At this stage, vertical divisions occur, followed by many irregular divisions which result in a massive, club-shaped suspensor.

THE HYPOPHYSIS

The hypophysis is differentiated in the linear embryo, occupying the fifth layer in an embryo of eight tiers (figs. 9, 10). Division of the hypophysis takes place about the time the embryo begins to take on its spherical form. The first walls are usually two vertical ones at right angles to each other so that a plate of four cells results. Exceptions, however, are shown in figures 11 and 20, where a horizontal wall was first formed. Horizontal division of the four-celled plate caused two layers to be formed, the upper layer extending laterally to complete the dermatogen, the lower layer forming the root-cap initials (figs. 20–22, 24). This corresponds to the behavior of the hypophysis of *Chenopodium bonus-henricus*.

Figure 17 illustrates a condition often seen in sections cut several cells thick. The upper part of the hypophysis bulges into the center of the embryo and seems to push the innermost cells upward as it does in *Capsella*.

THE DIFFERENTIATION OF THE HISTOGENS

The dermatogen is cut off early, usually when the third tier of the embryo consists of a quadrant of cells. A periclinal wall segments each of the four cells, and as the embryo enlarges, walls are formed in a similar position in the tiers above and below (figs. 11–14). The dermatogen is then complete except for that of the root tip which is to be formed later by the hypophysis as has been described.

The periblem is first distinquished when the embryo attains a diameter of five or six cells (figs. 12–14), as the row of cells just within the dermatogen. The remaining cells in the one or two rows at the center are those from which the plerome will be developed. As in *Chenopodium bonus-henricus*, the lowest tier of the embryo proper contributes the plerome and

periblem initials in the root. This situation is illustrated in figure 18. (The demarcation between the four tiers in the embryo is emphasized by heavier lines.) In older embryos (figs. 22, 24) distinction between the plerome and periblem is more easily made.

The formation of the histogens in *Kochia scoparia* as in *Chenopodium bonus-henricus* presents a variation from the *Capsella* type in which the periblem initials of the root tip originate from the uppermost half of the hypophysis.

LATER STAGES OF THE EMBRYO

The drawings in figures 28–35 illustrate the general outline of the embryo after the formation of the cotyledons. The bending of the embryo begins early (fig. 30) and continues until the tip of the innermost cotyledon meets the end of the root (fig. 35). The outer cotyledon does not increase in length to reach the end of the embryo-sac as it does in the similar horseshoe-shaped embryo of *Mirabilis jalapa* described by Woodcock (1928). It appears even shorter than the inner cotyledon because of its position on the periphery. In the mature embryo the length of the cotyledons is only slightly less than that of the hypocotyl and radicle.

Figure 22 shows an embryo when the cotyledons are well differentiated. All of the cells are large and tend to be isodiametric except for the procambium. The procambial strand forks at the apex, passing into the cotyledons for a short distance. At this stage no connection is made between the central strand and the plumule.

At the stage pictured in figure 32, the outline of the central strand is sharply marked (fig. 24), and the procambium extends about three-fourths of the distance to the tips of the cotyledons. No differentiation in size or shape of other cells in the cotyledon is seen at this stage (fig. 23).

Figures 25, 26, and 27 are sections from the mature embryo shown in figure 35. The median longitudinal section of the cotyledon (fig. 25), when compared with that in the figure above, shows a marked difference in cellular structure. Two or three rows of palisade parenchyma are indicated on the inner side of the cotyledon, which corresponds to the upper side when the cotyledon is expanded. A massive procambium running out to the tip of the cotyledon separates the palisade from large irregularly-placed cells on the opposite side of the cotyledon. Sections other than median ones show that the procambial strand is branched, indicating the course of the lateral veins in the leaf.

In figure 26 is shown a cross section of the procambial strand just below the point of forking. Figure 27 illustrates the forking of the central strand where the procambium passes into the cotyledons. The procambium is seen

to branch from the cotyledonary strand and enter the plumule. Although the formation of tracheary tubes does not occur in the embryo of the mature seed, the path of the procambium indicates that at the cotyledonary node the change from the protostele, typical of the root, to the siphonostele of the stem takes place.

DISCUSSION

Five types of dicotyledonous embryos are described by Schnarf (1928). The first is the Cruciferan, in which the apical cell of the two-celled embryo first divides vertically and in which the basal cell contributes only the suspensor and the hypophysis of the embryo. In the Asteracean type the apical cell also divides vertically, but the basal cell adds to the lower part of the embryo proper as well as forming the suspensor and hypophysis. The Solanacean, the Chenopodiacean, and the Caryophyllacean types are characterized by transverse division of the apical cell. In the first, however, the basal cell forms only the suspensor and hypophysis; in the second, it contributes the lower half of the embryo as well; and in the last, the basal cell does not divide at all but remains one-celled.

The embryo of *Chenopodium bonus-henricus*, as Souèges' drawings illustrate, represents the Chenopodiacean type. The resemblance of the embryo of *Kochia scoparia* to that of *Chenopodium bonus-henricus* indicates that its development also follows the Chenopodiacean pattern. Mitotic figures, however, were not observed in the critical stages, consequently the part played by each of the initial cells cannot be positively determined.

SUMMARY

1. The ovule of *Kochia scoparia* is campylotropous; at maturity the horseshoe-shaped embryo-sac surrounds a region of perisperm. There are two transparent integuments, the inner one protruding beyond the outer one at the micropyle.

2. The embryo-sac is early buried deep in the nucellus. It is eight-nucleate, although it is often seen with but two nuclei, the endosperm nucleus and the egg. This is due to the early disappearance of the antipodals and synergids, and the fusion of the polar nuclei.

3. The proembryo is characteristically linear, the vertical division of the apical cell being long delayed.

4. The spherical embryo is composed of four tiers, the upper two contributing to the plumule and cotyledons. The third, where the dermatogen is first cut off, contributes the hypocotyledonary region; the fourth, the plerome and periblem initials.

5. The hypophysis divides first vertically then horizontally. Two plates of cells are formed, the upper one of which by lateral extension of cells

completes the dermatogen, the lower one furnishes the root-cap initials.

6. The suspensor, at first two-celled, divides into four, the uppermost being the hypophysis. Transverse divisions take place rapidly, so that the suspensor becomes a long filament.

7. The endosperm is at first free-nuclear, forming two caps at the ends of the embryo-sac. Later, cells appear in the micropylar region which extend to the middle of the sac and form a loose covering over the embryo. The cap at the chalazal end remains free-nuclear and is finally obliterated by the growth of the embryo.

8. The embryo curves until in the mature seeds the tip of the innermost cotyledon meets the radicle.

9. In the mature embryo the solid procambial strand forks at the cotyledonary node and passes out to the tips of the cotyledons. As the procambium enters the cotyledon, a branch turns off which supplies the plumule.

The writer is indebted to Dr. E. R. Walker under whose direction this study was made, to Dr. E. N. Andersen for certain microchemical determinations, and to Prof. T. J. Fitzpatrick for the reading of the manuscript.

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Description of plates

(All figures drawn by means of the camera-lucida)

PLATE 25

Figs. 1–18. Series showing development of embryo through spherical stage; *h*, the hypophysis; heavier lines mark boundaries of the four tiers of the embryo. (All ×450.)

Fig. 19. Diagrammatic sketch of longitudinal section of young ovule; *a*, outer integument; *b*, inner integument; *c*, nucellus; lines and dots represent arrangement of cells of nucellus. (×65).

Fig. 20. Longitudinal section through embryo-sac of older ovule; endosperm caps shown, also disintegrating nucellar cells; *a*, outer integument reduced to one row of cells; *b*, inner integument represented as dark line, identity of cells having been lost; *c*, homogeneous suberized layer, represented as clear space; *d*, outer row of cells of nucellus. (×65).

PLATE 26

Fig. 21. Embryo with cotyledonary lobes and plumule forming; original outline of hypophysis indicated; plerome, periblem, and dermatogen distinctly marked. (×300).

Fig. 22. Stage with cotyledons well developed, procambium passing into them a short distance. Heavy lines emphasize regions of root tip. (×300).

Fig. 23. Median longitudinal section of cotyledon of the embryo shown in fig. 32. (×217).

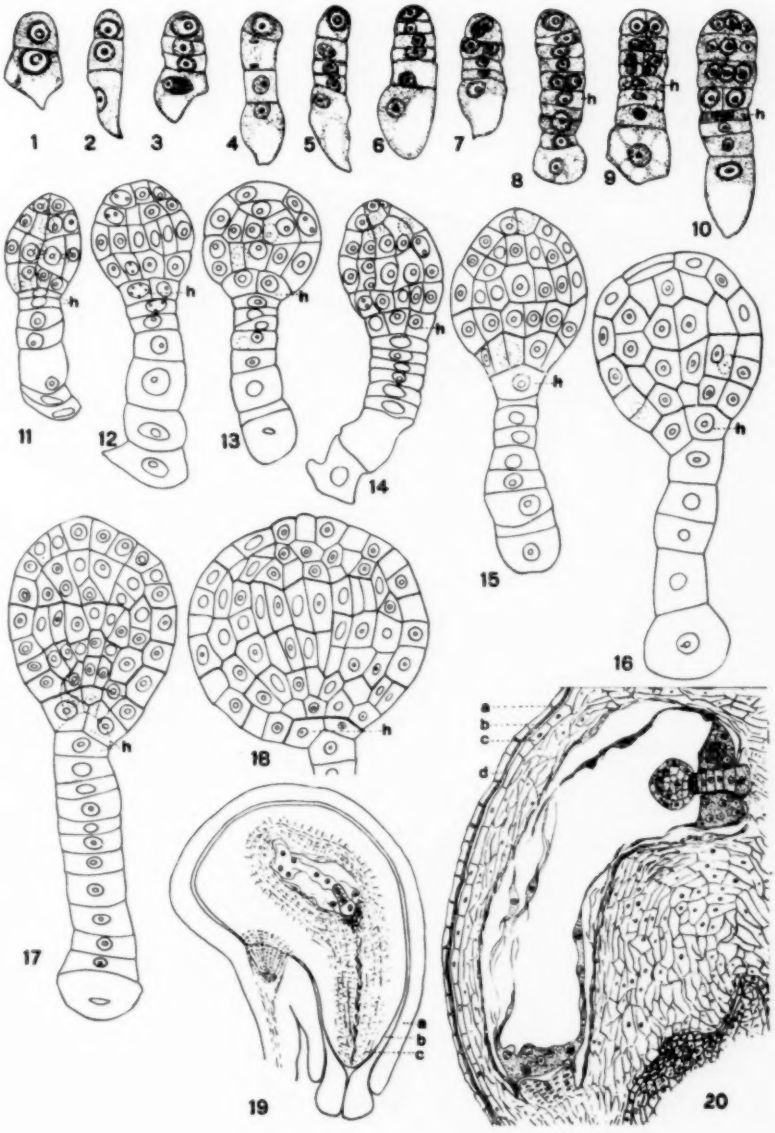
Fig. 24. Longitudinal section of radicle tip of same embryo, root cap initials shown. (×300).

Fig. 25. Median longitudinal section of cotyledon of mature embryo in fig. 35, showing differentiation of tissues. (×217).

Fig. 26. Cross section of central strand of mature embryo just below the point of forking. (×217).

Fig. 27. Median longitudinal section of mature embryo at cotyledonary node; procambium forks and passes out into the cotyledons; branch of cotyledonary procambium supplies the plumule. (×217).

Figs. 28–35. Series of outline drawings of embryo from appearance of cotyledons until maturity. (All ×20).



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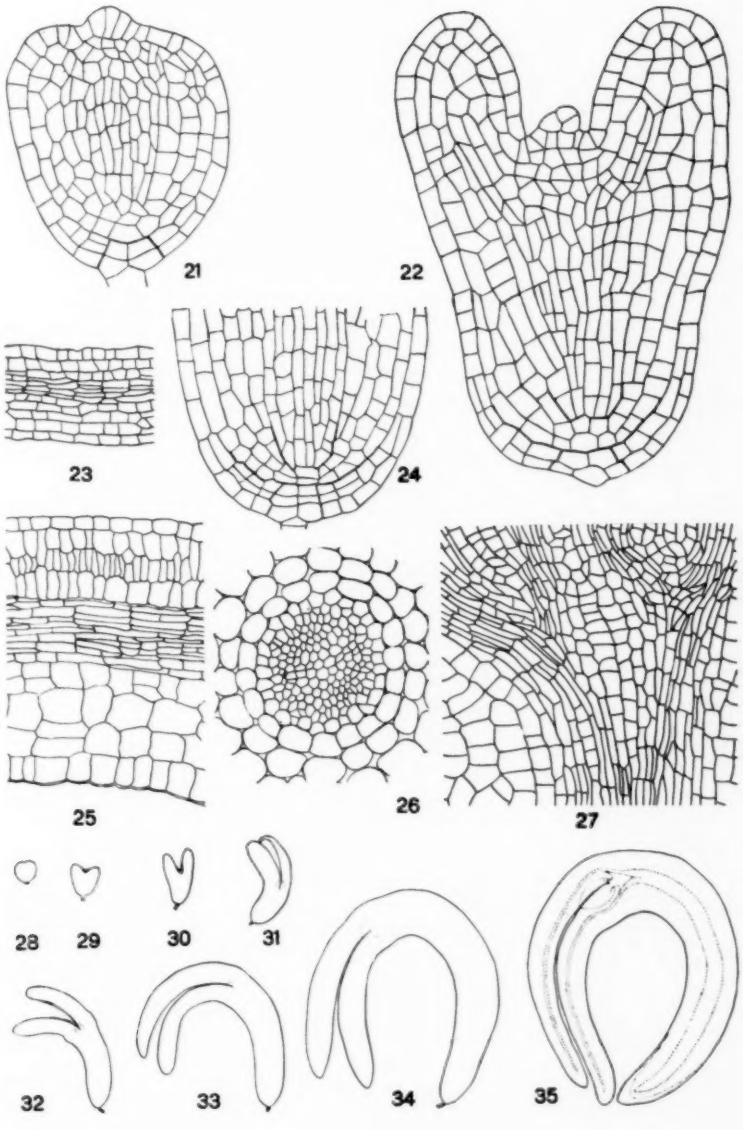

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Natural distribution of Rhododendron maximum in New Jersey[1]

ERNEST L. SPENCER
(WITH ONE TEXT FIGURE)

INTRODUCTION

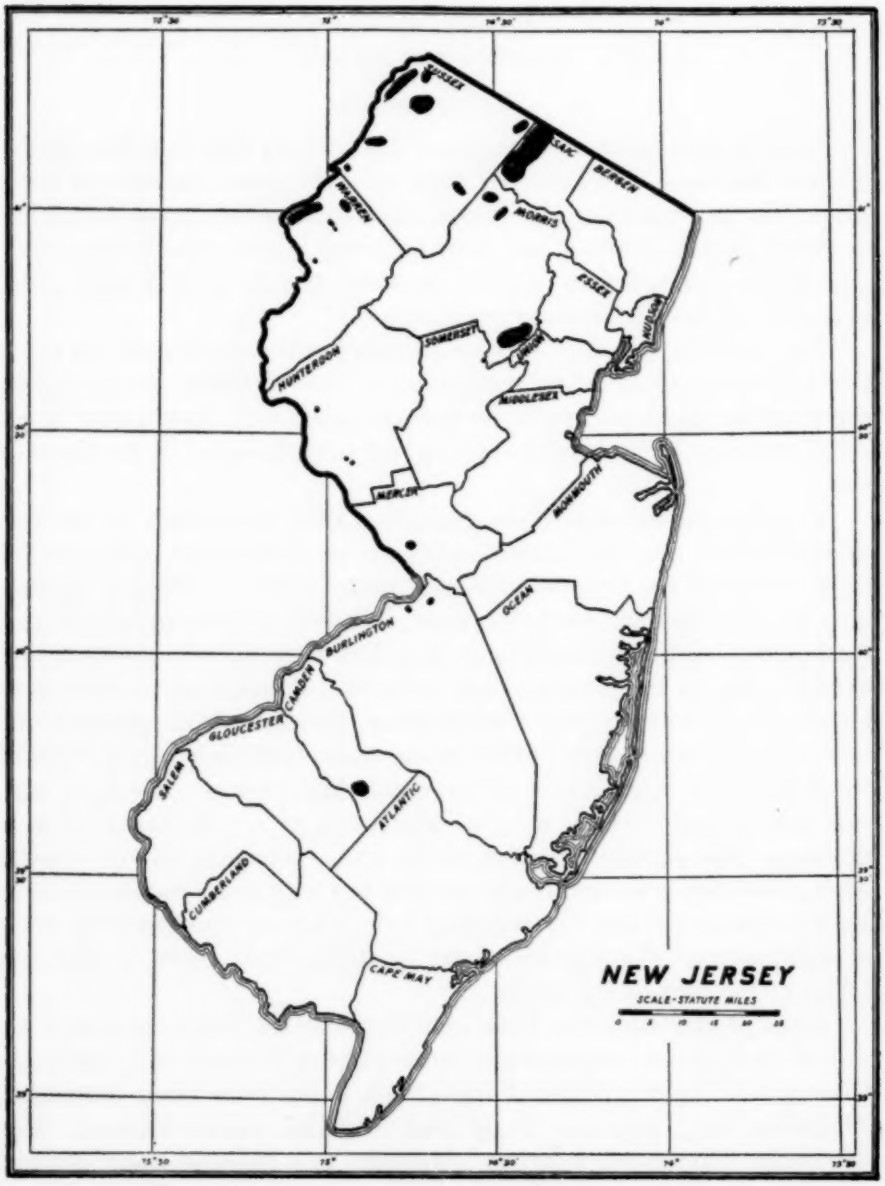
In sections of northern New Jersey one scarcely fails to notice *Rhododendron maximum L.* or Great Laurel, growing rather sparsely in some places but very extensively in others. *Rhododendron maximum*, a member of the Ericaceae, is one of our most beautiful plants. This woody shrub with its evergreen leaves and showy white or light pink flowers often reaches a height of from six to ten meters.

Why does this shrub grow so luxuriantly in the natural state but often lose its lustre and die when transplanted? This question has prompted the study of rhododendron in its natural habitats in New Jersey in an endeavor to ascertain what factors appear to be involved in its distribution.

The data here presented were obtained from 36 stations. A few stations may have been overlooked, but every stand which has been reported in the literature by Britton (1889) and Stone (1910), as well as many previously unrecorded stands, the locations of which were found with the help of local guides, were very carefully studied. The stations, with the exception of Sicklerville in the southern part of Camden County, are confined very largely to the northern and western areas. Rhododendron appears to be missing from the southern portion of the state. In the northern portion of the state, which forms a part of the Appalachian Province, are many narrow valleys and ravines, most of which run in a northeast-southwest direction. The southern portion of the state, belonging to the Coastal Plain, is relatively flat with very few hills but with many marshes bordering the stream courses. Observations were made on representative areas at each station. The map shows the locations where rhododendron was found at the time of this study.

Areas of rhododendron have been found in the following places, arranged by counties: Sussex-Wawayanda Plateau, Laurel Pond, Wallpack, Wawayanda, Sparta, Stokes Forest, High Point State Park, Montague, Flatbrookville, Dingmans Ferry and Millville; Passaic-Brown's, Moe Mountain, Uttertown, Bearfort Mountain, and Pinecliff Lake; Morris-Chatham Great Swamp, Milton and Copperas Mountain; Warren-Dunnfield, Pahaquarry, Hardwick and Blairstown; Hunterdon-Ramseysburg,

[1] Journal Series paper of the New Jersey Agricultural Experiment Station, Department of Plant Physiology.



Outline map of New Jersey showing the regions where Rhododendron maximum was found in the State

Stockton and Frenchtown; Mercer—Washington Crossing; Burlington—Bordentown and Kinkora; Camden—Sicklerville.

OBSERVATIONS

Because of the complexity of the factors which must be taken into account in attempting to explain the distribution of a plant, it appears advisable to consider some of these in detail. It should be understood, however, that the distribution of a plant is ultimately determined by a combination of these factors. In such a study it is necessary to explain not only the presence but also the absence of *Rhododendron maximum* in a particular locality. For clearness, the factors involved may be divided into two groups: environmental and edaphic.

Environmental factors.

As recorded in table 1 observations on the following environmental factors were made: topography, exposure, shade, proximity to water, depth of leaf mold, and drainage.

The data dealing with the topography of the stations where rhododendron grows appear at first sight to be inconsistent. A more careful study, however, reveals the fact that of the 29 principal stations, nine are in ravines, nine on hillsides or rocky cliffs, six on the banks of brooks, and five in swamps. The topography of these 29 stations is quite similar. With the exception of the swamp stations, rhododendron was found growing most luxuriantly in hemlock ravines.

This study shows that the manner of exposure is a factor of great importance to the distribution of rhododendron. Of the 29 principal stations all but five face to the north or northwest. These five exceptions are more or less flat areas; their lack of definite northern or northwestern exposures is probably compensated for by shade and humidity.

Observations made at Sparta, Wallpack and Brown's show to some extent the great significance of the exposure in the natural distribution of rhododendron, other factors being similar. Sparta Glen forms a deep east-and-west ravine in which *Tsuga canadensis* predominates. On the bank with a northern exposure rhododendron grows in great abundance. On the north bank, separated from the south bank at the base by a small brook not more than six to eight feet in width, there is not a single rhododendron plant. Soil reaction tests show a similar degree of acidity on both slopes. The exposure is the only apparent factor which distinguishes the north from the south slope and which could account for the clearly defined position occupied by rhododendron in this ravine. At Wallpack and Brown's, likewise, rhododendron is found growing in greater abundance on the slopes facing the north.

TABLE 1

Environmental factors characteristic of the different stands of Rhododendron maximum in New Jersey

STATION	TOPOGRAPHY	EXPOSURE	SHADE	PROX. TO WATER	LEAF MOLD	DRAINAGE
				FT.	IN.	
Abundant						
1. Brown's	Hemlock Ravine	N[a]	D[b]	Adja.	½	Good
2. Moe Mountain	Swamp	Flat	M	Adja.	3	Poor
3. Wawayanda Plateau	Cedar Swamp	Flat	M	Adja.	2	Poor
4. Chatham Great Swamp	Swamp	Flat	M	Adja.	4	Poor
5. Laurel Pond	Rocky Hillside	NW	D	Adja.	4	Good
6. Uttertown	Hemlock Ravine	NW	D	Adja.	4	Good
7. Wallpack	Hemlock Ravine	N	D	Adja.	1	Good
8. Bearfort Mountain	Rocky Hillside	N	D	Adja.	½	Good
9. Wawayanda	Hemlock Ravine	NW	D	Adja.	3	Good
10. Milton	Hemlock Ravine	NW	D	Adja.	3	Good
11. Sparta	Hemlock Ravine	N	D	Adja.	0	Good
12. Stokes Forest (A)	Rocky Hillside	N	M	200	1	Good
13. Dunnfield	Rocky Cliff	N	M	100	2	Good
14. High Point Park (A)	Bank of Brook	NW	M	Adja.	5	Good
15. Stokes Forest (B)	Hemlock Ravine	NW	M	Adja.	3	Good
16. Pahaquarry	Bank of Brook	NW	M	Adja.	½	Good
17. Montague (South)	Ravine	NW	M	200	3	Good
18. Sicklerville	Cedar Swamp	Flat	D	Adja.	5	Poor
Numerous						
19. Flatbrookville	Bank of Brook	NE	M	Adja.	1	Good
20. Dingmans Ferry	Hillside	NW	M	600	½	Good
21. Millville	Hillside	NW	M	600	3	Good
22. Montague (North)	Hemlock Ravine	NW	M	Adja.	1	Good
23. Stokes Forest (C)	Rocky Hillside	NW	M	750	2	Good
24. High Point Park (B)	Bank of Brook	W	M	Adja.	2	Good
25. Copperas Mountain	Rocky Hillside	NW	M	200	2	Good
26. Bordentown	Bank of Brook	N	M	Adja.	0	Good
27. Washington Crossing	Bank of Brook	N	M	Adja.	½	Good
28. Hardwick	Swamp	Flat	M	Adja.	5	Poor
29. Pinecliff Lake	Rocky Hillside	N	M	Adja.	2	Good
Scattered						
30. Kinkora	Steep Hillside	N	M	Adja.	1	Good
31. Ramseysburg	Hillside	N	M	100	2	Good
32. Stockton (A)	Bank of Brook	N	M	Adja.	3	Good
33. Stockton (B)	Bank of Brook	N	M	Adja.	1	Good
34. Frenchtown	Rocky Ravine	N	M	Adja.	2	Good
35. Blairstown (A)	Bank of Brook	NW	M	Adja.	1	Good
36. Blairstown (B)	Flat Woods	Flat	M	750	1	Good

[a] NW = northwest
N = north

[b] M = medium
D = dense

The sites where rhododendron grows most luxuriantly are characterized by a dense canopy of tree tops which permits very little direct sunlight to penetrate through to the ground below. Where the shade is less dense a mixed vegetation is found associated with rhododendron. Under such conditions *Kalmia latifolia* is also abundant. In no locality was rhododendron observed growing in dry exposed areas with little shade.

It is obvious that shade has a very marked influence on the external characters of rhododendron. In extremely dense shade the plants are straggly and crooked; the leaves are confined almost entirely to the new growth at the tips of the stems; the branches rarely grow more than one or two inches in length in any one season, and the number of blooms each season is comparatively small. In the less densely shaded situations the plants are more upright with thick, compact stems; the leaves extend more or less all along the stems but are of a lighter shade of green; the branches make as much as six to eight inches of terminal growth each season, and produce many blooms. The new growing tips of these plants are larger in diameter with more red pigment than those growing in the more densely shaded areas.

In deep ravines such as are found at Sparta, Wallpack and Brown's, the humidity is very high. The air is so saturated with moisture that the foliage often remains wet until noon or later even on bright days. In these stations an extensive development of fungi, mosses and ferns is observed and it is in such stations that rhododendron is the predominant type of undergrowth when other factors allow. Not all the stations are characterized by exceptionally high humidity, however, but this condition is always noted where the growth is most vigorous and healthy.

At nearly every station rhododendron grows in very close proximity to water, usually a small brook or stream. In only three cases was the shrub found to be at a considerable distance from water. These sites, for the most part, are on rocky hillsides.

The leaf mold at the several stations shows quite a decided variation in depth. This deposit often extends to a depth of five inches. The two sites where no leaf mold is present are on very steep slopes. Without a doubt the erosion due to rain water is sufficient to remove all the leaves and partially formed leaf mold and thereby prevents the accumulation of any such material. Most of the regions which show the greatest depth of leaf mold are rather flat, thereby favoring the accumulation of leaves and their partially decomposed remains. The average depth of leaf mold at the 29 principal stations is about two inches.

There are but five exceptions to the general conclusion that good drainage is essential for the successful growth of rhododendron. This good

drainage is due in part, undoubtedly, to the texture of the soil, most of it being stony or gravelly. Although the soil is well drained, it appears to have an adequate supply of moisture. At Moe Mountain, Chatham, Wawayanda Plateau, Hardwick and Sicklerville, rhododendron grows in swamps.

Edaphic factors.

Schimper (1898) has given the name *edaphic* to those factors dealing with the soil and its peculiarities. These factors as recorded in table 2 are soil texture and soil reaction.

Several different soil series of the stony or gravelly type seem to be well suited to the growth of rhododendron. The soil series of each station was identified by reference to the soil survey maps of New Jersey by Jennings (1911), Lee (1921), and Patrick (1917, 1919). In addition to the rocky outcrops the soil series on which rhododendron was found are Lackawanna, Hoosic, Gloucester, Penn, Collington, Culvers, Dutchess, Wallpack, and Bermudian. No *Rhododendron maximum* was found in New Jersey on soils of limestone origin.

From the data as recorded in table 2 it is quite apparent that the acidity of the soil is of considerable importance as a factor in the distribution of rhododendron. At each station the reaction of the leaf mold, of the soil to a depth of six inches, and of the soil to a depth of twelve inches was determined. This twelve inch limit was arbitrarily selected since the roots of rhododendron seldom penetrate below this depth. With respect to the leaf mold the reaction varies from pH 5.2 to pH 2.9, with an average of pH 4.0. The acidity for the first six inches of soil ranged from pH 4.8 to pH 2.9, giving an average pH of 4.0. For the second six inches the reaction ranged from pH 4.8 to pH 2.9, with an average pH of 4.2. In view of the fact that rhododendron was not found on soil with a reaction above pH 5.6, it is concluded that this plant has a natural "preference" for acid soils.

Associated flora.

In a study of the flora occurring with *Rhododendron maximum*, it may be advisable to discuss first the species, as given in table 3, which are found in most of the stations, and then to consider in detail some of the representative larger stands.

Tsuga canadensis is associated more characteristically with rhododendron than any other species of trees. There are only ten stations in which *Tsuga canadensis* is missing. At least one species of *Quercus* may be identified with all but seven stands. Among the principal species of *Quercus* are *Q. alba*, *Q. velutina* and *Q. Prinus*. Among the species of *Acer* found associated with rhododendron, *Acer rubrum* occurs most frequently, being pres-

TABLE 2

Edaphic factors characteristic of the different stands of Rhododendron maximum

STATION	SOIL TEXTURE	HYDROGEN-ION CONCENTRATION		
		LEAF MOLD	LEAF MOLD–6"	6"–12"
		pH	pH	pH
Abundant				
1. Brown's	Hoosic gravelly loam	5.1	4.8	4.7
2. Moe Mountain	Muck	3.2	3.6	4.2
3. Wawayanda Plateau	Muck	3.6	4.0	4.1
4. Chatham Great Swamp	Muck	2.9	3.0	2.9
5. Laurel Pond	Gloucester stony loam	4.0	3.9	—
6. Uttertown	Lackawanna stony loam	4.1	3.6	3.9
7. Wallpack	Rock outcrop	4.2	4.3	4.3
8. Bearfort Mountain	Rough stony land	4.7	4.3	4.1
9. Wawayanda	Gloucester stony loam	3.9	3.3	—
10. Milton	Gloucester stony loam	3.5	—	—
11. Sparta	Gloucester stony loam	—	4.7	4.8
12. Stokes Forest (A)	Lackawanna stony loam	3.5	3.7	4.0
13. Dunnfield	Rock outcrop	4.0	—	—
14. High Point Park (A)	Lackawanna stony loam	4.8	—	—
15. Stokes Forest (B)	Lackawanna stony loam	4.9	—	—
16. Pahaquarry	Lackawanna stony loam	4.9	4.1	4.4
17. Montague (South)	Hoosic gravelly loam	3.6	3.9	4.3
18. Sicklerville	Muck	3.1	3.0	—
Numerous				
19. Flatbrookville	Hoosic gravelly loam	5.2	4.1	4.4
20. Dingmans Ferry	Wallpack fine sandy loam	4.8	4.5	4.4
21. Millville	Wallpack stony loam	4.1	4.1	3.9
22. Montague (North)	Hoosic gravelly loam	3.7	4.5	4.2
23. Stokes Forest (C)	Lackawanna stony loam	5.2	4.1	4.0
24. High Point Park (B)	Lackawanna stony loam	4.3	3.9	4.1
25. Copperas Mountain	Rough stony land	4.0	3.7	—
26. Bordentown	Collington sandy loam	—	2.9	3.6
27. Washington Crossing	Bermudian silt loam	5.0	4.5	4.1
28. Hardwick	Muck	4.2	4.2	—
29. Pinecliff Lake	Hoosic gravelly loam	3.4	4.3	—
Scattered				
30. Kinkora	Collington loam	3.3	3.8	3.5
31. Ramseysburg	Dutchess shale loam	4.6	4.4	4.3
32. Stockton (A)	Penn shale loam	5.0	4.1	4.3
33. Stockton (B)	Penn gravelly loam	3.9	3.5	—
34. Frenchtown	Penn shale loam	4.7	4.4	4.3
35. Blairstown (A)	Dutchess shale loam	5.0	4.7	4.5
36. Blairstown (B)	Culvers loam	4.8	4.6	4.5
	Average	4.0	4.0	4.2
	Range High	5.2	4.8	4.8
	Range Low	2.9	2.9	2.9

TABLE 3

The relative abundance of the various species associated with Rhododendron maximum in its natural stands

STATION	RHODODENDRON MAXIMUM	KALMIA LATIFOLIA	TSUGA CANADENSIS	ACER RUBRUM	CORNUS FLORIDA	QUERCUS ALBA	QUERCUS VELUTINA	QUERCUS PRINUS	BETULA LENTA	BETULA LUTEA	FAGUS AMERICANA	LIRIODENDRON TULIPIFERA	CHAMAECYPARIS THYOIDES
1. Brown's	P	N	P	S	S					S	S	S	
2. Moe Mountain	P	N	P	S	S					S	S		
3. Wawayanda Plateau	P		P	S		S		S	S	S			N
4. Chatham Great Swamp	P	N		S	S	S			S		S	S	
5. Laurel Pond	P		P	S						S	S		
6. Uttertown	P	N	P	S	S					S	S		
7. Wallpack	P	N	P	S	S	S			S				
8. Bearfort Mountain	P	N	P	S	S	S				S			
9. Wawayanda	P	N	P	S	S					S			
10. Milton	P	N	P	S	S	S				S			
11. Sparta	P	N	P	S		S			S	S			
12. Stokes Forest (A)	P	N		S				S		S			
13. Dunnfield	A	S	P	S	S			S	S				
14. High Point Park (A)	A	N	N	S	S	S	S	S	S				
15. Stokes Forest (B)	A	N	P	S		S	S	S		S		S	
16. Pahaquarry	A	N	S	S	S	S		S	S		S	S	
17. Montague (South)	A			S		N	S	S					
18. Sicklerville	P			S		S	S						P
19. Flatbrookville	N	N	P		S	S	S		S		S		
20. Dingmans Ferry	N	N	S	N	S	N	S	S					
21. Millville	N	A	N	S	S		S	S					
22. Montague (North)	N		N	S			N					S	
23. Stokes Forest (C)	N	N	P	S	S	N		S	S	S		S	
24. High Point Park (B)	N	A	N	S		S	S	S		S			
25. Copperas Mountain	N	A	S	S		S	S	S					
26. Bordentown	N			S	S		S				S	S	
27. Washington Crossing	N			S	S								
28. Hardwick	N	N	S	S	S	S	S	S	S				
29. Pinecliff Lake	N	N	N	S	S			P			S		
30. Kinkora	S			S	S		S		S		S	S	
31. Ramseysburg	S	N	N			S							
32. Stockton (A)	S			S	S				S				
33. Stockton (B)	S		N	S			N						
34. Frenchtown	S		N	N		S	S						
35. Blairstown (A)	S	N		S	S	S		S	S	S		S	
36. Blairstown (B)	S	N		N		S			S				
Total	36	25	26	34	22	21	15	15	14	14	10	9	2

P=predominant, A=abundant, N=numerous, S=scattered.

ent in 34 stations. *Acer saccharum* and *A. pennsylvanicum* are also found with several of the stands. *Cornus florida*, *Betula lenta* and *B. lutea* are present frequently, as well as scattered groups of *Liriodendron tulipifera*, *Fagus americana*, *Pinus Strobus*, and *Chamaecyparis thyoides*.

Very few different species of shrubs are present in many of the stations. *Kalmia latifolia* thrives in all but eleven of the stations where rhododendron is found. In a few of the larger areas rhododendron is the only shrub present. Isolated groups of *Viburnum*, usually *V. acerifolium*, *Hamamelis virginiana*, *Clethra alnifolia*, and *Vaccinium pennsylvanicum* are found. With the exception of the mosses and saprophytic fungi, there appears to be very little characteristic ground vegetation.

For a more detailed account of the vegetation associated with rhododendron at the different stations, it may be advisable to select a few typical sites rather than to discuss each stand separately.

At Brown's is found a typical ravine with a true hemlock formation. This ravine, which extends in a northeast to southwest direction, has a small brook with high slopes on either side. The soil here is described as rough, stony land of the Hoosic series with good under-drainage. In addition to the vigorous growth of rhododendron at the bottom of the ravine there is a stand of *Tsuga canadensis*, with only a few scattered specimens of *Fagus americana* and *Acer rubrum*. These trees are able to withstand the dense shade of the hemlock, in which rhododendron thrives. In regard to the slopes it is immediately apparent that the vegetation of one slope is different from that of the other. On the slope facing northward are found *Rhododendron maximum* and *Kalmia latifolia*, thriving beneath the dense canopy of the hemlock. This association extends far up the slope. On the opposite slope with a southern exposure a different condition is encountered. Here the forest is more of the maple-beech-hemlock type, made up of *Acer rubrum*, *Fagus americana* and *Tsuga canadensis*, with some *Cornus florida*, *Betula lutea* and *Liriodendron tulipifera*. Rhododendron, as well as hemlock, disappears a short distance up this slope.

At Wallpack similar conditions with respect to exposure prevail. At the bottom of the ravine there is a hemlock formation with an undergrowth consisting almost exclusively of *Rhododendron maximum*. On the rocky cliffs along the brook, which extends up through the ravine, are found associated with the hemlock, as secondary species since they are tolerant of shade, *Betula lenta*, *Acer rubrum*, *A. pennsylvanicum*, *Cornus florida*, and *Quercus alba*. As the stand of trees thins out *Kalmia latifolia* makes its appearance. On the slope facing northward is found an abundant growth of rhododendron, whereas on the opposite slope this species is absent, a

condition similar to that observed at Brown's and apparently due to the same causes.

At Dunnfield rhododendron grows in a different type of topography. Throughout the entire length of the Delaware Water Gap the rhododendron is very prominent, growing in great abundance on the rocky cliffs overlooking the Delaware River to the northwest. Here the forest is of the hemlock-deciduous type with *Tsuga canadensis*, *Acer rubrum*, *A. pennsylvanicum*, *Cornus florida*, *Quercus Prinus*, and *Betula lenta*. The cliffs are very steep and rough and give rise to little streams of water which run as from springs. The vegetation in general is quite straggly and crooked, as though subjected to severe winds.

On Moe Mountain another condition may be observed. At the top of the mountain is a large swamp in which rhododendron is very abundant. Associated with it and forming a rather open type forest is *Tsuga canadensis* and *Betula lutea*. Here the rhododendron appears very vigorous, forming a somewhat dense thicket of undergrowth. Along the margins of the swamp together with the extensive development of rhododendron, are *Quercus Prinus*, *Cornus florida*, *Kalmia latifolia* and *Myrica asplenifolia*. On the slopes arising from the swamp the same abundant growth of rhododendron as at Brown's and at Wallpack was observed on the slope facing northeast, but none at all on the opposite slope. North of the swamp both hemlock and rhododendron disappear at about the same elevation.

In a cedar swamp at Sicklerville, the southernmost station found in New Jersey, there is a very exceptional colony of rhododendron. Stone (1910) describes this station as follows: "The white cedars rose on every hand like tall columns, their dense tops shutting off much of the light, and under them, with tangled and twisted trunks and branches, grew the Rhododendrons, the masses of white blossoms standing out conspicuously against the dark leaves and the general gloom. The high humidity, the absolute lack of motion in the air, and the low basin-like character of the spot made it extremely oppressive and the atmosphere seemed fairly reeking with moisture. I have suffered from excessive perspiration in the *Rhododendron* thickets of the Alleghenies much as I did that day (July 9, 1910) in the cedar swamp, and perhaps the similarly humid conditions are what the plant needs." The absence of *Tsuga canadensis* is very conspicuous.

Seedlings. The seedlings of *Rhododendron maximum* are found in only a very few stations. There are very extensive stands of healthy seedlings at Moe Mountain on the elevated margins of the swamp, at Wallpack in the upper ravine, at Stokes Forest on the partially exposed hilltop, and at Chatham on the small knolls in the Great Swamp.

DISCUSSION

The results of these observations indicate that some of the factors studied seem to be more significant than others. Of these factors there are three which warrant further consideration: (1) soil reaction, (2) exposure, and (3) seed germination. The question of the relative importance of soil reaction and exposure in this connection is still open to discussion. The data already presented have shown that one cannot be separated from the other for it is the apparent combination of both these factors which seems to restrict the natural distribution of rhododendron.

If it is justifiable to draw conclusions from the observations made at 36 stations, it is evident that rhododendron "prefers" an acid soil. Whether or not this is a limiting factor in the distribution of rhododendron is hard to say, for this apparent "preference" has not been fully demonstrated as yet by experimental evidence. Several tentative explanations for this condition have been advanced by various workers. The acid reaction may render available some elements such as iron, which in small quantities are required for growth. Unpublished experimental evidence with solution cultures (Spencer 1932) has shown that an acid medium is essential only in rendering available some nutritive elements which are insoluble in a neutral or alkaline medium. In regard to soils, however, the experimental evidence is still too superficial to warrant drawing any definite conclusion as to the manner in which an acid reaction may function. Perhaps the same symbiotic relation, which has been demonstrated by Dufrenoy (1917) and Rayner (1923) to exist between other members of the Ericaceae and mycorrhiza, exists also between these organisms and rhododendron. If this is the case, an acid reaction may favor increased fungal activity, whereas an alkaline medium may retard its development. The fact that rhododendron is not found on the limestone soils south of Vernon on the northwest slopes of Wawayanda Mountain and similar locations in New Jersey, where other factors for the natural development of this species are apparently favorable, is evidence in support of the theory that soil acidity is an important factor in the distribution of rhododendron.

The importance of a proper exposure is very well brought out by the data already presented. The fact that no stand of rhododendron was found with a southern exposure may be based on the environmental characteristics of both the northern and southern exposures. The factors involved are undoubtedly light intensity, temperature, and humidity. On the northern exposure the light intensity is naturally lower than on the southern because the direct rays of the sun reach it at a more acute angle and for a shorter period each day. As a result of this shorter exposure to direct sunlight the temperature is normally lower. The humidity, on the other hand,

is higher since less evaporation occurs. All three of these factors are favorable to the growth of rhododendron. Winter injury is undoubtedly a significant factor in the distribution of rhododendron since it is a matter of common observation that this type of injury is much more prevalent on the southern exposure than on the northern. This is due to the frequent freezings and thawings on the southern exposures, a condition known to be quite injurious to all but the most hardy types of vegetation.

Several interesting observations were made concerning the manner in which rhododendron reproduces in the wild. It has been demonstrated experimentally by seed germination tests that the seeds are viable. Data obtained at the various stations indicate that the seedlings are highly specific in their environmental requirements. These requirements appear to be (1) a relatively high humidity, (2) a moderate exposure such as is offered by a lightly wooded forest, and (3) a soil reaction between pH 3.5 and 5.0. It is probable that in very dense shade the young seedlings cannot synthesize adequate carbohydrates to carry them through the first winter. It may also be that germination is retarded to such an extent in these areas by the lower temperature that the seedlings are not sufficiently developed at the end of the growing season to withstand the severe conditions of winter. Evidently rhododendron now growing in the dense shade of the hemlock started while these trees were still small. A count of the annual rings at the base of several of these shrubs showed that many of these larger rhododendron plants are at least 65 years old.

From the data presented it appears that the conditions under which rhododendron thrives are quite similar to those required by *Tsuga*. This undoubtedly accounts for the close association between these two species. Both species appear to thrive in the same type of environment. Harshberger (1911) describes the hemlock as a tree which thrives on the rocky sides of mountain gorges, or a rocky hillside overlooking a stream. Occasionally it appears in a deep forest on the flat ground by a stream. It grows on the slopes facing the north rather than on the southern slopes and hilltops. These conditions coincide with the apparent natural conditions required by rhododendron. The *Tsuga* has been found, however, in limestone soil in New Jersey, whereas rhododendron has never been found on such soils.

SUMMARY

1. In the State of New Jersey 36 natural stands of *Rhododendron maximum* were located, mostly in the northern and western regions of the state. In five localities the shrub grows in swamps: at Moe Mountain, Waway-

anda Plateau, Chatham Great Swamp, Hardwick, and at Sicklerville, the latter being the southernmost station in the state.

2. The distribution of rhododendron seems to be governed by its specific topographical requirements rather than by climate. It appears to prefer ravines or rocky hillsides although several stands were found along the banks of small brooks.

3. In every station rhododendron grows on acid soil and never on limestone soil. The soil reaction of the several stations is decidedly acid, the range extending from pH 5.2 to pH 2.9.

4. The significance of exposure is well brought out, especially by the stands situated in ravines. In these stations there is an extensive development of rhododendron on the slopes facing north, whereas on the opposite slopes the shrub is absent or restricted to the base of the slope. None of the 36 stations has an exposure to the south.

5. The most luxuriant growth of rhododendron is noted in localities characterized by dense shade and high humidity.

6. In New Jersey rhododendron is commonly associated with *Tsuga canadensis* and *Kalmia latifolia*.

7. Young seedlings were found in only five of the 36 stations where the larger plants are now growing. Inasmuch as germination tests showed that seeds are viable, it is evident that the seedlings themselves must be highly specific in their environmental requirements. The factors involved appear to be humidity and light intensity as well as soil reaction.

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Department of Plant Physiology
New Jersey Agricultural Experiment Station
New Brunswick, N. J.

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The development of the ascocarp in two species of Thielavia

C. W. Emmons

(with one text figure and plates 27 and 28)

The members of the medical profession, in their studies of skin diseases especially, have accumulated much knowledge regarding species of fungi parasitic on man. Forms causing thrush, ringworm, sporotrichosis, and coccidioidal granuloma, are among those well known to the medical mycologist, but not always so familiar to those botanists concerned purely with problems of plant pathology or with fungi as a whole. There are in human pathology, just as in plant pathology, cases where it is difficult to say whether the trouble in question is primarily due to the particular fungus isolated, working as a parasite, or whether it may not simply be aggravating the original trouble in a secondary capacity. The tendency in former years has been for medical mycologists to be rather conservative and to disregard fungi other than those long known to be primary parasites, the effects of which present definite clinical pictures. More recently they have been studying culturally and experimentally those fungi occupying the border line between parasitism and saprophytism. One may cite cases where the spores of fungi familiar to the botanist, such as *Puccinia graminis*, *Penicillium glaucum*, *Alternaria Mali*[1] and others, have been proved to be the cause of asthmatic attacks in certain individuals. It is now conceded that certain cases of ear and lung troubles are due to infection by species of *Aspergillus*.

Such lines of work call for much more extended knowledge of those fungi, not only on the part of those interested in human diseases, but on the part of the botanist as well. A survey was recently organized by Dr. R. M. McLaughlin of the College of Physicians and Surgeons, Columbia University, with the primary object of learning to what extent certain groups of college students were infected with the fungi which cause ringworm of the foot. In this survey it was planned to obtain cultures, not only from those individuals with clinical lesions, but also from those who appeared to be normal. The fungi appearing in these cultures included forms known to be pathogenic, and many which probably had no etiologic significance. Most of these latter were undoubtedly represented in the lesions or on the skin merely by a few air borne and ungerminated spores which grew as soon as planted upon the culture medium. A study of these cultures has resulted in the discovery of a number of interesting forms, among which was a new species of *Thielavia* isolated by Dr. McLaughlin

[1] Hopkins, J. G., R. W. Benham, and B. M. Kesten. 1930. Asthma due to a fungus—*Alternaria*. Journ. Amer. Med. Assoc. **94**: 6–10.

from the normal skin of a foot. He has kindly permitted the author to make a special study of this fungus which is considered to be a saprophyte and no great importance is attached to its source, although related forms are met with frequently as contaminants of cultures similarly made. The studies reported here were all made from strains derived from single spores.

In an earlier paper[2] I have given a brief account of *Thielavia terricola*. Further study has seemed to show that the ascogenous hyphae of that species produce croziers from the penultimate cells of which the asci develop. Some of the salient feature of its development are to be mentioned in this report which is devoted principally to a description of another species of *Thielavia* mentioned above and hitherto undescribed, although it is apparently closely related to *T. terricola*. This relationship is manifested by similarities in the manner of growth in the early stages of ascocarp formation, in the character of the mature ascocarp, and in the appearance of asci and ascospores. In the second species, however, the ascogenous hyphae develop no croziers and there is apparently no nuclear fusion in the ascus. One or the other or both of these remarkable features have been reported in other groups of fungi; the interest here lies in the fact that while one species of *Thielavia* goes through the usual stages in the formation of ascospores, a second closely related species has a very much shortened life history.

Thielavia terricola (Gilman and Abbott) Emmons

The ascocarp of *Thielavia terricola* develops from a hyphal coil. The coil as well as the hypha which bears it and the hyphae which soon surround it are somewhat difficult to distinguish even when stained with aceto-carmine. There does not appear to be any antheridium. Single spore cultures produce ascocarps. The coil soon becomes surrounded by an envelope of hyphae, but it remains visible through these as a deeply staining structure made up of from one to three cells. The coil grows as the young ascocarp develops and there is an increase in the number as well as in the size of the cells. It soon gives rise to a branching system of ascogenous hyphae. The asci appear to develop from the penultimate cell of a crozier and nuclear fusion occurs at the very beginning of ascus formation. Fusion of the ultimate and the antepenultimate cells could not be demonstrated. There is no uniformity in the orientation of the ascogenous hyphae and asci. The former grow out from the coil which is located at a point near the center of the ascocarp and the asci may point in any direction. This arrangement corresponds in general to that in *Microascus trigonosporus* and

[2] Emmons, C. W. 1930. *Coniothyrium terricola* proves to be a species of *Thielavia*. Bul. Torrey Bot. Club. **57**: 123–126.

M. intermedius[3] except that in *Thielavia terricola* the ascocarp is smaller but the asci are larger, and consequently the radial development of the system is less noticeable. The first asci to mature are near the center of the cleistocarpous fruiting structure, and in a maturing ascocarp, ascogenous hyphae can be found only next to the perithecium. No open central cavity forms but the nurse tissue is destroyed lysigenetically as the fertile hyphae and asci advance. Three nuclear divisions occur and eight spores are cut out. The ascospores are elliptical with a germ pore at only one end.

Thielavia Sepedonium sp. nov. Emmons.

Mycelio homothallico; perithecio globoso, 70–150μ diametro, pariete exteriori olivaceo; ascis ovoideis, 17–30μ, e ramis lateralibus hypharum asciferarum orientibus, sine nucleorum conjugationibus, 8-sporis; ascosporis ellipticis olivaceis, 7–10$\times$14–19μ, poro germinali ad vertices ambas.

Conidiis sphaericis, interdum ovoideis, 7–10μ diametro, tuberculato-papillatis, singulatim vel in catenis brevibus ad conidiophoros ramosos proventis.

Thielavia Sepedonium is so much like *T. terricola* in the general appearance of the mature ascocarp, asci, and ascospores that the advisability of describing it as a different species was at first questioned. However it grows more rapidly and luxuriantly than *T. terricola;* it has a conspicuous conidial stage; and there are very important differences in the ascocarpic development, in the ascospores, and in the perithecial wall cells. The character of the conidia would place this fungus in the genus *Sepedonium* Link, of the Fungi Imperfecti. Of the species of this genus it most closely resembles *S. albo-luteum*, but it differs from that species in important respects noted in the description. The perfect stage, when present, should determine the taxonomic position and the name of a fungus, and the ascocarp which is a prominent feature of this fungus is that of a *Thielavia*. The specific name *Sepedonium* is proposed here in order to suggest the type of its conidial stage.

Thielavia Sepedonium develops rapidly upon cornmeal agar with the formation of a scanty gray mycelium. Within four days at 30°C, in monospore cultures, ascocarps are visible as tiny black spots on the surface of the agar, and by the fifth day many of the asci contain spores. As in many ascomycetes, the ascocarps form more quickly and in greater abundance on plate cultures of cornmeal agar if inoculations are made at several points. On dextrose and other sugar media there is a stronger development of aerial mycelium which becomes golden yellow with the production of great masses of conidia, and finally grayish over most of the colony with

[3] Emmons, C. W., and B. O. Dodge. 1931. The ascocarpic stage of species of *Scopulariopsis*. Mycologia **23**: 313–331.

the formation of ascocarps. The conidia are borne upon branched conidiophores (plate 27, a–e). The spores arise from swollen portions of the conidiophore (plate 27, c), which swellings, in many cases at least, in turn become conidia. The conidia appear to be solitary, but short chains sometimes form. The conidium is at first borne upon a little stalk and is smooth. Later, as the spore increases in size the stalk disappears and the surface becomes covered with tuberculate thickenings. The spores are spherical, 7–10μ in diameter, or sometimes egg-shaped and up to 8$\times$12μ in size.

The ascocarp develops from a hyphal coil (plate 27, f–i). No antheridium is present. The ascocarp is spherical, 70–150μ in diameter, and without an ostiole. The perithecium, the wall portion of the ascocarp, is composed (a) of a single layer of pigmented cells whose outer walls are deeply sculptured (plate 28, d) and (b) two or three layers of thin-walled flattened cells. At the center of the young fruit body one finds a number of pseudoparenchymatous cells which are eventually destroyed as the asci develop (plate 28, h). The asci, about 17$\times$30μ, arise as side branches on the ascogneous hyphae. Each ascus contains eight ascospores which are elliptical, darkly olivaceous, 7–10$\times$14–19μ, with a germ pore at each end (plate 27, j) as contrasted with the ascospores of *T. terricola* which have only one germ pore. They remain uninucleate until germination.

In the development of the ascogenous hyphae there is at no stage any suggestion of a crozier. The growth is straight out from the original coil (text fig. 1 and plate 28, h). Each cell of the ascogenous hyphae is uninucleate except the tip cell which, just before cell division in the course of hyphal growth, becomes binucleate. Cells which are about to form branches from which asci are to be cut are also binucleate, but the ascus cell has only one nucleus when it is cut off (plate 27, l). Growth is apical as is clearly shown by the progressive development of asci along an ascogenous hypha (text fig. 1), and binucleate tip cells are occasionally seen. The ascogenous hyphae branch freely at first and binucleate cells are sometimes found at the base of a young branch. The young branch is initiated before nuclear division; after nuclear division one nucleus passes into the branch and a wall is laid down. The ascus arises in the same manner as a branch (text fig. 1 and plate 27, l), and in some cases it is difficult to be sure whether one is observing a young branch or a young ascus. In most cases it is possible to tell by noting the stage of development of the ascogenous hypha and of the asci arising from the older cells of the ascogenous hypha. If the ascocarp is well developed and ascogenous hyphae have penetrated to all parts of its interior, and if several nearly mature asci are present, further branching of the ascogenous hyphae does not occur.

The young ascus first appears two or three cells distant from the tip

(text fig. 1) and the general appearance is quite different from what one finds in *T. terricola* where the ascus appears to arise from the penultimate cell of a crozier. In *T. Sepedonium* one of the daughter nuclei passes into the young ascus (plate 27, l) which is cut off by a wall. Ascus and nucleus increase rapidly in size, but there is no preliminary binucleate stage or nuclear fusion. When the ascus reaches its mature size there are the three usual nuclear divisions. Many mitotic figures of each of the three nuclear divisions have been secured. The chromosome number seems to be four. Each of the nuclei now cuts out a spore by free-cell formation. Many preparations of a later stage show the nucleus attached to the spore wall by a long beak as described by Harper[4] for the powdery mildews. Later the nucleus rounds up at the center of the spore. The spore, which is at first spherical, later becomes ellipsoidal and it has a germ pore at each end (plate 27, j). It remains uninucleate until germination begins.

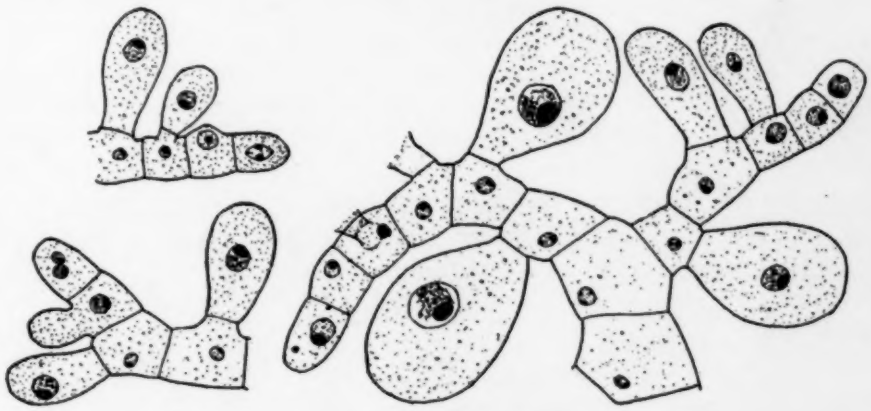


Fig. 1. Stages in the formation of the asci of *T. Sepedonium*.

The remarkable and interesting cytological features in the life history of *T. Sepedonium* are the lack of crozier or ascus crook, and the absence of a nuclear fusion in the young ascus. While the crozier can not be demonstrated in certain ascomycetous forms the nuclear fusion in the ascus is a commonly and easily observed phenomenon which is usually thought of as being universal among the higher ascomycetes. No nuclear fusions are reported to occur in some of the reduced forms such as the 4-spored yeasts and species of Endomycetaceae. It seems probable that an adequate study of many of the reduced forms among the Plectascales will show still other species where crozier formation and nuclear fusion are dispensed with.

[4] Harper, R. A. 1895. Ueber das Verhalten der Kerne bei der Fruchtentwickelung einiger Ascomyceten. Jahrb. f. Wiss. Bot. **29**: 655–685.

If a crozier is present in the mildews it is in a reduced form and it seems quite certain that in some species it is lacking. However the nuclear fusion in the ascus is well known since Harper's[4] work on these forms. Wingard[5] in a study of *Nematospora Phaseoli*, the cause of a spot disease of the lima bean, found no nuclear fusion in the ascus. The only nuclear fusion known for other yeasts is that between the nuclei of the copulating cells in such forms as *Schizosaccharomyces octosporus*, and corresponds therefor to the first nuclear fusion in such forms as the mildews.

Among the Basidiomycetes there are several species where basidia form only two basidiospores and no nuclear fusion is known to occur. In *Caeoma nitens*[6] and *Endophyllum Euphorbiae-sylvaticae*[7] the nuclear fusion which usually precedes the formation of the promycelium in the rusts is lacking.

SUMMARY

Cytological data are given for two species of *Thielavia*. *T. Sepedonium* is described as a new species. It forms its asci as simple side branches from the ascogenous hyphae without crozier formation and without nuclear fusion in the ascus. *T. terricola* resembles *T. Sepedonium* superficially but in the former the asci appear to arise from the penultimate cell of a crozier which is binucleate.

I am indebted to Dr. B. O. Dodge for assistance and advice during the course of this study, and to Prof. R. A. Harper for assistance in the interpretation of the cytological details.

[5] Wingard, S. A. 1925. Studies on the pathogenicity, morphology, and cytology of *Nematospora Phaseoli*. Bul. Torrey Bot. Club. **52:** 250–290.

[6] Dodge, B. O. 1924. Uninucleate aecidiospores in *Caeoma nitens* and associated phenomena. Journ. Agr. Res. **28:** 1045–1058.

[7] Moreau, Mme. F. 1914. Les phénomènes de la sexualité chez les Urédinées. Botaniste. **3:** 145–284.

Explanation of plates

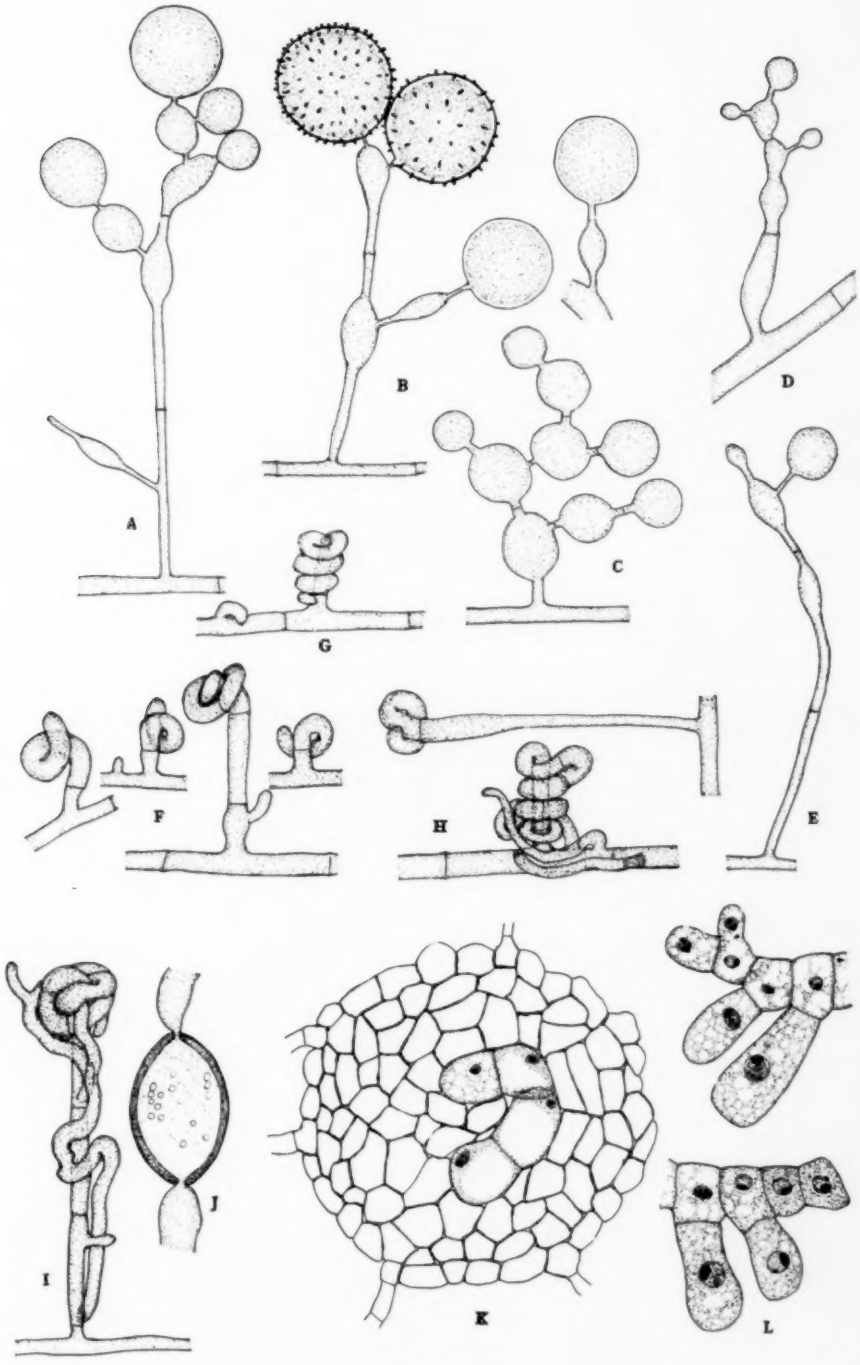
PLATE 27

Thielavia Sepedonium

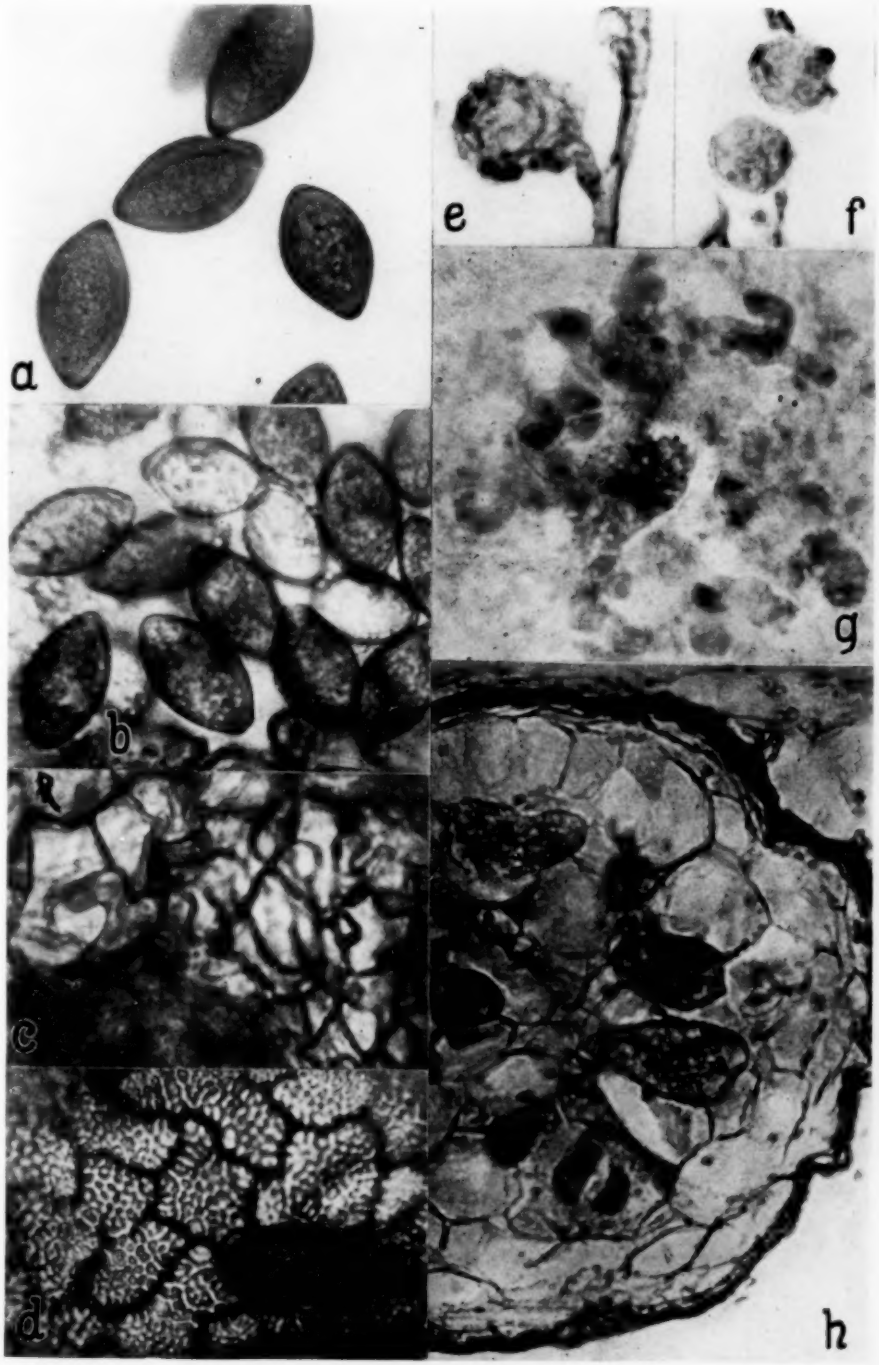
a-e, conidiophores and conidia.
f-i, ascogonial coils.
j, germinating ascospore.
k, young ascocarp showing ascogonium with uninucleate cells.
l, ascogenous hyphae bearing young asci.

PLATE 28

a, ascospores of *Thielavia Sepedonium*.
b, ascospores of *T. terricola*.
c, wall cells of the perithecium of *T. terricola*.
d, wall cells of the perithecium of *T. Sepedonium*.
e, young ascocarp of *T. Sepedonium*.
f, conidia of *T. Sepedonium*.
g, aceto-carmine preparation of crushed mount of ascogenous hyphae of *T. terricola*.
h, section of ascocarp of *T. Sepedonium*.



EMMONS: THIELAVIA


a
b
c
d
e
f
g
h

Regeneration in a sweet cherry leaf

V. A. Young

(with plate 29 and one text figure)

Much has been written relative to the underlying causes of regeneration in plants, but as yet no general definition or theory has been advanced which is wholly accepted by workers as an explanation for such phenomena. Among the investigators who differed widely as to the definition of regeneration as applied to their respective problems, certain definite groups stand out quite distinctly. One of these groups includes Prantl (1874), Němec (1905), and Pfeffer (1905), who contended that regeneration is the formation of a new part or parts exactly alike in number and position of the organs injured or removed. Another group of workers, Vöchting (1878), Goebel (1902), Morgan (1901), and Klebs (1908), consider regeneration to be the development of additional organs from dormant buds present before an injury occurs. Miss Kupfer (1907), one of the more recent investigators, suggests that the term regeneration be limited to those cases in which an organ is formed, de novo, at a place or under conditions in which it would not normally be found.

The definition suggested by Miss Kupfer seems to cover quite adequately the occurrence of an unusual case of regeneration associated with the outgrowth on a leaf of sweet cherry (*Prunus avium* L.) brought to the attention of the writer during the early summer of 1931. This leaf (pl. 29) appeared normal in all respects with the exception of six small leaf-like structures (for convenience these structures will henceforth be called leaflets) on the lower surface.

From general observations each leaflet appeared as an individual unit, but after a careful examination with a hand lens it was obvious that each leaflet was composed of two small outgrowths extremely close to each other. A dark longitudinal line appears in the approximate center of each supposedly complete leaflet. This line represents the area separating the two leaflets. The manner in which the leaflets were attached to the main leaf was unique, each being firmly held near the inner edge and along the entire length of its blade, but free elsewhere. The specific areas from which the leaflets originated on the leaf could not definitely be determined from observations made with low magnification. The evidence obtained from these observations did, however, strongly indicate that the leaflets had their origin in the leaf veins. Such evidence was later confirmed from the studies made of microscopic sections from the areas supporting the regenerated organs. Both the leaf and the leaflets were rich in chlorophyl,

but their colors were distinctly different. The pigmentation of the leaf produced a deep brownish green color, while the color of the leaflets was a brilliant green. A pronounced differentiation in the external morphology of the leaf and leaflets was also apparent. In the former, as illustrated in plate 29, the margin of the blade is serrated while the margins of the leaflets facing each other are entire, but deeply lobed on the outer free edges. The venation also varies widely in both leaf types, the veins of the leaf radiating from the midrib, while there is no midrib present in the leaflets.

Microscopic sections were made of all leaf areas supporting regenerated leaflets. The usual histological methods were used.[1] The general anatomical structure of a cross-section of one of these areas is illustrated in figure 1 by a drawing made with a Promar drawing apparatus. The anatomy of the leaf in the region of the regeneration is highly diversified as compared with

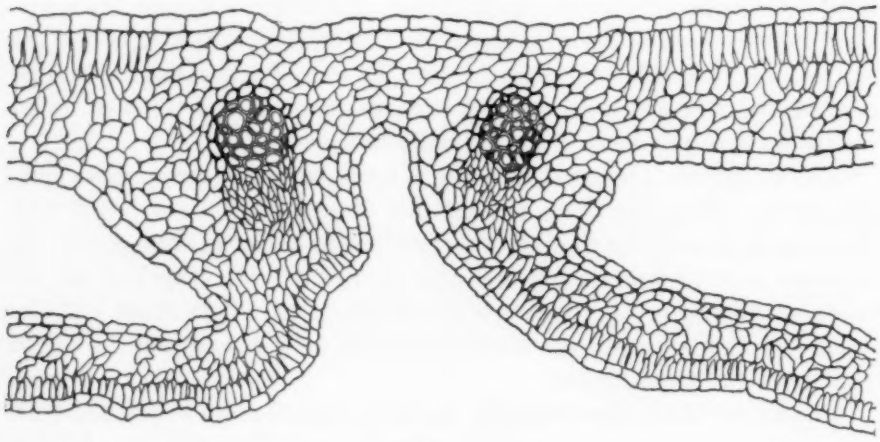


Fig. 1

the normal areas. This is due to the fact that two separate and distinct vascular systems are formed by the dichotomous branching of the vein (secondary veins) and being discontinued with the region of regeneration. The anatomical features of these secondary veins are also highly diversified as compared with the primary vein, the phloem tissue in each case being unusually large. In addition the mesophyll tissue between as well as surrounding the two veins is composed of large irregular and closely congested parenchyma, which has apparently replaced the palisade layer of the leaf directly above the two veins for some distance along the margin. One of

[1] Many helpful suggestions were offered by Dr. H. F. A. Meier, head of the Botany and Pathology Department, in the preparation of the histological material.

the undetermined anatomical complexities was the initial origin of the two secondary veins from the primary vein. All of the microscopic sections taken in the leaf tissues both near and including the region of the regenerated organs show no anatomical differences which might indicate the specific area or tissue where the division first occurred. In every section a sharp boundary separated the two secondary veins from the primary vein where a transitional area might be expected. It is highly possible, however, that a transitional area did exist in the young developing leaf when regeneration first occurred, but later the differentiation of the cells had obliterated all traces of the origin of the tissues involved. The microscopic study did, however, clearly show that the first external appearance of the regenerated leaflets was definitely correlated with the presence of the secondary veins. Furthermore the anatomical structure of the secondary veins strongly indicated that the phloem tissue was involved in the reproduction of the additional leaflets. As stated elsewhere the phloem tissue is unusually large and the cells appear to blend gradually into a system of parenchymatous tissue of the small leaflets. From such evidence one might conceive that the phloem tissue of the initial vein is the source of origin of the secondary veins. The anatomical features of the leaflets, as illustrated in figure 1, are similar to those of the leaf except that the palisade layer of the former is reversed in position with that of the latter.

Since the anatomical data discussed represent conditions found in a mature leaf supporting regenerative organs, it is only possible to postulate as to the specific cells or tissues involved in the regeneration. A young leaf exhibiting similar characteristics at a very early stage would unquestionably solve the problem. Nevertheless the data discussed above definitely indicate that regeneration may occur in plant tissues which show no evidence of external injury. Furthermore the anatomical evidence of the mature leaf does not indicate that dormant buds were present before the additional organs were formed. Moreover the evidence is quite conclusive that regeneration induces pronounced anatomical changes where it occurs, regardless of the specific cells or tissue responsible for the origin of the new organs. It is highly possible that certain physiological reactions not clearly understood play a major rôle in causing regeneration.

The literature shows that a profound interest has been aroused among biologists in the subject of regeneration. Much progress has been made in this phase of biology; nevertheless, much more is still to be accomplished before any definite theories can be formulated relative to the underlying causes of regeneration. With this realization in mind it has been the hope of the writer that the data presented might encourage other investigators to seek further for additional information relative to the complexities of

regeneration, a phenomenon more common in nature than is generally realized.

FOREST BOTANY AND PATHOLOGY
THE N. Y. STATE COLLEGE OF FORESTRY
SYRACUSE UNIVERSITY

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YOUNG: REGENERATION

...IV. OF ...ICH.

Field and herbarium studies, I

LOUIS WILLIAMS

In working up a collection of plants which the writer and Miss Rua Pierson made in and near Grand Teton National Park during the summer of 1931, attention was called to the *Phacelia* and *Corallorrhiza* as probably new. The *Eriogonum* species were received from A. O. Garrett and given to the writer by Doctor Aven Nelson for study. The following species have been carefully compared by myself, under the direction of Doctor Nelson, with material in The Rocky Mountain Herbarium.

Corallorrhiza purpurea L. Williams sp. nov. Caulis carnosus, ruber, 2 dm. altus; racemus cum 20–30 floribus; planta glabra; flores 1.5 cm. longi; labium circa 8 mm. longum, purpureum, cum 2 lobis lateralibus; pollinia 4; sepala subviridia, subaequalia; petala similia.

Scape red, fleshy, 2–4 dm. high with 2–3 membranaceous sheaths. Raceme 20 to 30-flowered, compact when young, less so with age; root coralloid; plant glabrous throughout; flowers about 1.5 cm. long; lip about 8 mm. long, purplish, faintly 3-nerved or only the central nerve visible, with a basal lobe on each side which may be bifid, there may also be some serrations between the lobes and the apex of the lip; column about 4 mm. long, to which are attached four pollinia by a central filament, two on each side of the filament, waxy, easily detached; sepals three, greenish, subequal, the lateral ones forming a short spur, which is less than 1 mm. long, faintly 3-nerved or apparently not at all; petals similar to the sepals, often tinged with purple.

This species somewhat resembles *C. Mertensiana* Bong. It differs in that *C. purpurea* L. Williams has a lobed lip which may also have some serrations, the column is shorter, and it usually has more flowers in the raceme.

Type specimen collected by Louis Williams and Rua Pierson in moist shaded situations, near Bradley Lake, Grand Teton National Park, June 22, 1931. Coll. No. 199. Type in Rocky Mt. Herb.

Eriogonum crispum L. Williams sp. nov. Perenne ligneum, ramosum, praeter 3 dm. altum, ascendens; cortex concisurus, tomentosus; folia oblonga, crenata, tomentosa infra alba, prope vel omnino glabra supra, fasciculata ad caulem veterem, alternata ad incrementum annuum; inflorescentia cymosa; involucrum circa 1 mm. longum, campanulatum, pubescens, 5–8-denticulatum, dentes subfusci; perianthum flavum, glabrum; filamentum ad basin villosum.

A coarse, diffusely branched, woody perennial. More than 3 dm. high; bark somewhat shreddy, appearing white from tomentum, probably becoming more or less glabrous with age; stems ascending; leaves short-petiolate, oblong, 2–3 cm. long, 3–7 mm. broad, crenately crisped giving the appearance of serrations, densely white tomentose below, sparingly so or glabrous above, mostly

fascicled on the older stems, alternate on the annual growth, approaching within 4–6 cm. of the inflorescence which is a multi-compound-cymose umbel; involucre about 1 mm. long, campanulate, pubescent, 5–8-toothed, tips of the teeth brownish; perianth stipitate, bright yellow; segments about 1 mm. long, equal, obtuse-ovate, glabrous; filament villose at the base, as long as the perianth.

A very pretty form of woody *Eriogonum* collected by A. O. Garrett in Cedar Canyon, Iron County, Utah, September 2, 1931. Coll. No. 6027. The specimen in hand is 3 dm. tall, the plant from which it was taken was probably 4–6 dm. or more. Type in Rocky Mt. Herb.

Eriogonum filiformum L. Williams sp. nov. Annuum ramosissimum; caulis filiformis, 1–2 dm. altus, aliquot ex caudice, glabri; nodi amplificati et angulosi; folia omnia ad basin, lamina oblonga, 1–4 cm. longa, tomentosa infra et supra prope vel omnino glabra; involucra 0.5–1 mm. longa, axillaria, pubescentia, campanulata, cum paucis floribus; pedicelli circa 5 mm. longi vel pauci sessiles in axi; lobi obtusi, breves, subrubro-gilvo ad rubidum; segmenta aequalia; bracteae squameae.

A diffusely di-trichotomously branched annual. The stems gradually diminishing in size until they are almost filiform, 1–2 dm. high; main branches several from the caudex, glabrous; the nodes enlarged and angled; leaves all basal, leaf blades 1–4 cm. long, oblong, tomentose below, sparsely so or glabrate above; petiole 2–5 cm. long; involucres 0.5–1 mm. long, axillary, pubescent, campanulate, few flowered; pedicels of the involucres mostly about 5 mm. long or a few sessile in the axis; lobes obtuse, short reddish; perianth reddish-yellow to dark red; segments equal, obtuse; bracts scale-like.

Collected west of Hawksville, Wayne County, Utah, July 23, 1931, by A. O. Garrett. Coll. No. 5975. Type in Rocky Mt. Herb.

Eriogonum Nelsonii L. Williams sp. nov. Perenne ligneum, praeter 2 dm. altum, breviter et dense tomentosum plus minus glabrescens cum aetate; folia lineari-revoluta, 0.5–1.5 cm. longa, infra tomentosa, plus minus glabra supra; petioli breves vel nulli; inflorescentia multi-cymoso-umbellata; involucrum 1–2 mm. longum, viride vel fuscum, villoso-pubescens, campanulatum, acutilobum; perianthum album cum vena viridi in quoque lobo.

A woody perennial, more than two dm. high, with shreddy bark. Densely short tomentose, more tomentose from the base toward the tip and becoming more or less glabrous with age; leaves linear-revolute, 0.5–1.5 cm. long, appearing mucronate, some of the leaves of the perennial growth fascicled, alternate on the annual and ascending within 4–8 cm, of the inflorescence, all densely woolly-tomentose on the lower side, less so or glabrous above; petiole very short or absent; inflorescence a few involucral heads (10–40) in a compound-cymose-umbel; involucre 1–2 mm. long, green or brown, villose pubescent, campanulate; lobes acute; perianth white with a green vein in each lobe; lobes ovate, 1 mm. or less long, equal; stamens almost as long as the perianth;

anthers red, nodding; filament pubescent; flowers stipitate, 4–10 in each involucral head.

It is with pleasure that I dedicate this species to Dr. Aven Nelson; first because of the generous help which he has at all times given me; secondly because he had spent some time on the type when it was received and had designated it as probably new.

The type specimen was collected by Ernest P. Walker, July 30, 1912, in a dry sandy park, Geyser Basin, San Juan County, Utah. Coll. No. 368. The co-type specimen was collected by A. O. Garrett at Cedar Canyon, Iron County, Utah, September 2, 1931. Coll. No. 6028. Type and co-type in Rocky Mt. Herb.

Phacelia Piersoniae. L. Williams sp. nov. Bienne erecta, 2–4 dm. alta, sine ramis, pubescens; folia caulis petiolata, integra, lineari-lanceolata, pubescentia; calycis lobi hirsuti, lineares, 3 mm. longi, acuti; corolla alba, glabra, 4–6 mm. longa; inflorescentia hispido-hirsuta, scorpioidea; ovarium hirsutum; stylus divisus ad medium.

Biennial with a short tap-root. Stems strikingly erect, 2–4 dm. high, unbranched, only one stem from each tap-root, pubescent; cauline leaves petiolate, entire, linear-lanceolate, tapering to the petiole and acute at the tip, 4–8 cm. long, pubescent on both sides, more so above than below, veins well pronounced on the lower side, less so above, leaves of the preceding year forming a rosette at the base of the stem, more or less pubescent; calyx lobes hirsute, more so on the margins than in the center, narrowly linear, about 3 mm. long, acute; corolla white, glabrous, 4–6 mm. long, fading to ochroleucous in drying; inflorescence hispid-hirsute, consisting of several short-peduncled scorpioid spikes; filaments 6–8 mm. long, sparsely pilose, exserted, attached near the base of the corolla tube, alternate with the lobes; anthers versatile; ovary densely hirsute, ovate; style almost as long as the stamens, cleft to the middle.

This species is probably closely related to *P. nemoralis* Greene. It resembles somewhat the description of *P. leptosepala* Rydberg, which Doctor Brand, in his monograph on the *Hydrophyllaceae*, reduces to *P. nemoralis* Greene. It differs in that *P. nemoralis* Greene is perennial, has ascending stems and a more or less caespitose rootstalk.

The type was collected on the STS Ranch, Moose, Jackson Hole, Wyoming, June 26, 1931. Coll. No. 223 (Louis Williams and Rua Pierson). Co-type collected in Grand Teton National Park, along the trail above Bradley Lake, June 24, 1931. Coll. No. 359 (Louis Williams and Rua Pierson). It is dedicated to the co-collector. Type and co-type in Rocky Mt. Herb.

UNIVERSITY OF WYOMING
LARAMIE, WYOMING

INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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